Running head: Loss of persistence along an herbivory gradient

# Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory

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ABSTRACT (247 words).

Overabundant white-tailed deer (*Odocoileus virginianus*) are a significant management problem in North America that exert unprecedented herbivory pressure on native understory forest communities. Conserving understory plant populations requires quantifying a sustainable level of deer herbivory. To date, most population projection models consider only deer presence and absence. To estimate population growth rate along a gradient of herbivory, we focused on *Trillium grandiflorum* because it is a common understory species and a bellwether of deer effects and forest decline. We used matrix population models, and employed both prospective and retrospective analyses using a regression life table response experiment (LTRE).

Deer affect size, stage and population dynamics of *T. grandiflorum*. Because deer target flowering and large non-flowering stages of *T. grandiflorum,* these individuals do not produce seed in the year they are browsed and are more likely to regress in stage and size in the following growing season relative to non-browsed plants. Importantly, sustained high browse levels result in populations dominated by small, non-flowering individuals. Our LTRE revealed a significant negative and decelerating relationship between herbivory and λ. This non-linearity occurs at the highest herbivory levels because highly browsed populations become dominated by stages that deer do not consume and are thus buffered from rapid decline. However, population extinction is expected when herbivory is greater than the pivotal value of ~15%. Our study demonstrates that levels of deer herbivory commonly experienced by forest understory perennials are sufficient to cause the loss of *T. grandiflorum* and likely other co-occurring palatable species.

Keywords: demography, elasticity analysis, extinction risk, interspecific interactions, matrix model, tolerance

INTRODUCTION

Increases in the density of white-tailed deer (*Odocoileus virginianus*), and the resulting increase in herbivory of forest understory plants, is a striking example of human-mediated change in a biotic interaction (McCabe and McCabe 1997, Russell et al. 2001, Côté et al. 2004). Habitat fragmentation, the eradication of large carnivores, and the increase in food resources from modern agricultural practices, among other factors, have resulted in dense populations of white-tailed deer (henceforth deer) throughout eastern North America (McCabe and McCabe 1997). Because deer are generalist herbivores, most palatable forest understory species are currently experiencing unprecedented herbivore pressure (McCabe and McCabe 1997, Russell et al. 2001, Côté et al. 2004). Worldwide, deer and other large ungulate browsers threaten forest and agricultural ecosystems because their dense populations can inhibit forest plants' regeneration and reduce crop yield (Tilghman 1989, Inouye et al. 1994, Waller and Alverson 1997; Persson et al. 2000; Rooney 2001, Russell et al. 2001, Augustine & DeCalesta 2003, Horsley et al. 2003, Côté et al. 2004).

Deer densities in North America are currently 2- to 4-fold above historical records (McCabe & McCabe 1997). High local deer densities have been shown to reduce overall plant biomass, shift community composition from more to less palatable plant species, and dramatically reduce overall plant biodiversity (Russell et al. 2001, Rooney and Waller 2003, Côté et al. 2004, Wiegmann and Waller 2006, Royo and Carson 2006). Deer-mediated decline of many previously abundant herbaceous understory species has created conservation concern (e.g. Miller et al. 1992, Anderson 1994, Balgooyen and Waller 1995, Augustine and Frelich 1998, Augustine et al. 1998, Anderson et al. 2001, Rooney and Gross 2003, Rooney and Waller 2003, Côté et al. 2004). This concern is supported by the results of demographic matrix model

analyses that demonstrate that high levels of deer herbivory can lead to increased extinction risk of plants (Rooney and Gross 2003, Knight 2004, McGraw and Furedi 2005).

Most native forest species that are palatable to deer have long generation times and experience stage-specific browsing. For example, many trees are vulnerable to deer herbivory as seedlings, but reach size refugia as saplings (Russell et al. 2001). In contrast, herbaceous understory plants often experience greater herbivory at larger, reproductive stages (Augustine and Frelich 1998, Rooney and Gross 2003, Knight 2003, 2004, McGraw and Furedi 2005, Jenkins et al. 2007). In order to quantify the effects of such stage-specific herbivory on plant population dynamics, a stage-structured population model is required.

Typically, effects of deer herbivory on understory plants have been examined experimentally using fenced exclosure and control plots (e.g. Alverson et al. 1988, Augustine and Frelich 1998, Augustine et al. 1998, Anderson et al. 2001, Townsend and Meyer 2002). These studies show large positive effects of deer exclusion on the growth, survival and reproduction of plants. However, because these experiments typically are conducted in a single site by erecting exclusion and control plots, they cannot provide information regarding plant responses across a natural gradient of herbivory. Likewise, separate matrices can be constructed for all plants in a population (browsed and not browsed) vs. only those plants that are not browsed. Comparison of the population dynamics and persistence derived from the two matrices provides insight into the direct and indirect effect of deer (all plants) vs. only the indirect effects (Knight 2004). Both of these approaches examine the effects of complete deer removal on the plant population dynamics. Unfortunately, the complete cessation of deer herbivory in natural areas is not a reasonable or desirable management option (Girard 1993). However, determining the critical level of herbivory that allows population persistence would provide useful

information for managers. In this study, we collected field data in 12 natural populations of the long-lived herb *Trillium grandiflorum* and analyzed it using demographic matrix population model projection analyses. These populations experience a gradient of deer herbivory, which permits us to determine the relationship between per capita herbivory rates on *T. grandiflorum* and plant demography.

Specifically, we ask: (1) What are the relationships between deer herbivory and *T. grandiflorum* vital rates, population growth rate ($\lambda$), stage structure, reproductive value, and elasticities? (2) How do each of the vital rates contribute to the effect of herbivory on $\lambda$? To answer these questions we develop a set of matrix population models that express the vital rates as functions of herbivory. We use a life table response experiment (LTRE) analysis to decompose observed variation in $\lambda$ into contributions of variation in each of the vital rates. Because the level of herbivory is a continuous variable, we employed a regression design LTRE (Caswell 1996, 2001); this is the first application of the LTRE regression method to a wild population (see Caswell 1996 for a laboratory study).

## METHODS

### Study Species and Sites

*Trillium grandiflorum* white trillium (Melanthiaceae; Zomlefer et al. 2001) is a preferred food of deer (Anderson 1994, Augustine and Frelich 1998) and is an excellent indicator species for determining sustainable deer browse level in forests (Anderson 1994, Augustine and DeCalesta 2003, Knight 2004). Despite the fact that many *T. grandiflorum* populations are suspected to be declining in size, this species remains a ubiquitous component of deciduous forests understories throughout eastern North America (Case and Case 1997). Two prior studies

applied a demographic matrix approach to *T. grandiflorum*, and both showed that deer herbivory is a critical factor that determines population persistence (Rooney and Gross 2003, Knight 2004). Thus, the deer impact threshold that allows for the persistence of *T. grandiflorum* populations should also support the persistence of other, less preferred herbaceous species in the same community.

In our northwestern Pennsylvania populations, *T. grandiflorum* emerges in early spring, before the forest canopy leafs out, and above-ground parts die back in mid-summer. Reproductive plants bloom for 2-3 weeks (late April to mid-May). This species is a non-clonal perennial, with distinct lifecycle stages (described below) that are easily distinguishable in the field (Kalisz et al. 2001, Knight 2003, 2004). Deer primarily consume reproductive or large 3-leaf stage *T. grandiflorum*, typically removing all leaf and flower tissue (Knight 2003). Complete defoliation does not usually cause mortality, but plants are unable to re-sprout until the following growing season (Augustine and Frelich 1998, Knight 2003, Rooney and Gross 2003). Flowering plants that are eaten by deer lose all reproductive success for the current growing season and are more likely to regress back to a non-reproductive stage in the following growing season (Knight 2003, 2004).

We collected data from 12 populations of *Trillium grandiflorum* representing a range of habitat sizes and aspects typical of northwestern Pennsylvania, USA. The sites vary in a variety of factors besides the intensity of herbivory, however, all 12 sites are in deciduous forests with an overstory dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and red oak (*Quercus rubra*). Our study populations were separated by 4 km to 55 km (Knight 2003).

Projection matrix estimates

**Transitions of plants after emergence**—In each population, we set up between 5 and 27 1-$m^2$ plots, located along a single transect. The number of plots and the distance between plots (between 10 and 50 m) depended on the density and extent of the *T. grandiflorum* population in a site (see Knight 2004 for site descriptions). The TW population was an exception; 9 transects were necessary due to the high dispersion of the plants at that site. In April 1999, we tagged and classified all *T. grandiflorum* plants within each plot by stage: seedling (a single cotyledon), 1-leaf (plants with one true leaf), 3-leaf (vegetative plant with a whorl of three leaves) and reproductive (plant with whorl of three leaves and a single flower). In addition, we tagged plants in rare stages in extra plots, until either a sample size of 40 individuals was reached for each stage, or until all plants of a stage in that population were tagged. In 1999-2002, we censused all plots to document the stage and size (estimated by leaf length) of each tagged plant, and to tag new seedlings. The structure of these *T. grandiflorum* populations is categorized by six stage-size classes (detailed below). Censuses were carried out in late April, when the plants first emerged, and before deer consumed any plants. In total, we monitored 2993 plants across all 12 populations.

After the first census, all tagged plants were checked for deer herbivory at least every other week and more frequently early in the season. Deer browsed *T. grandiflorum* can be distinguished from that of other herbivores because deer lack top front teeth so they tear vegetation, often at a horizontal angle. Rodents and lagomorphs create sharp cuts on the stem, typically at a 45 degree angle. Herbivory by species other than deer accounted for less than 1% of the observed consumption of *T. grandiflorum*.

**Fecundity--** Reproductive plants that were consumed by deer were scored as having no

seed production. For all other reproductive plants, we recorded successful fruit set and counted the number of seeds in the fruit. Fruits were collected each year in early July, shortly before the fruits would naturally drop from the plants. We improved our fecundity estimates in populations with high herbivory by collecting fruits from randomly selected reproductive plants outside of our demography plots. We calculated average fecundity per individual as (average number of seeds/reproductive plant) X (proportion of reproductive plants not browsed).

**Seed germination**—*T. grandiflorum* seeds express double-dormancy (Baskin and Baskin 2001): seeds germinate, but only the radicles emerge in their first year. Seedlings appear above ground as in the second year post germination. In order to follow the fate of seeds, in 1999 we established seed baskets in each population by placing 30 seeds into 25-$cm^3$ seed baskets constructed of 1-mm mesh fiberglass screening and filled with sieved soil from the field site. Sample size for each population was 20 seed baskets. The TW population had so few fruiting plants that only 10 seed baskets could be established. We collected one half of the seed baskets in May of 2000, one year after they were installed, sieved the seeds from the soil, and counted the number of germinated seeds. This allowed us to calculate the probability of a seed surviving one year and germinating (hereafter, germination probability). Because counting the number of germinants (germinated seeds) required destructive sampling, these individuals could not be followed any further. In 2001, we counted the number of seedlings that emerged from the remaining 10 seed baskets/population. The probability that a germinated seed survives to the seedling stage (hereafter, seedling emergence probability) was calculated as the proportion of seeds surviving two years divided by the germination probability.

Demographic Analysis

We created a population projection matrix for each population in each year, using the transition

probabilities of vegetative plants from 1999-2000, 2000-2001 and 2001-2002, the average seed production in 1999, 2000, 2001 and 2002, and the estimates of seed fates from seed baskets in 1999. We defined 6 stages: germinant (1), seedling (2), 1-leaf (3), small 3-leaf (4), large 3-leaf (5), and reproductive (6), to create the life cycle graph shown in Figure 1. Small three leaf plants ($\leq$5cm leaf length) can regress to the 1-leaf stage but cannot advance to the reproductive stage, while the opposite is true for large (>5 cm leaf length) 3-leaf plants. Both 3-leaf and reproductive plants can enter a dormant stage, in which they remain below ground for one or more growing seasons (Hanzawa and Kalisz 1993). However, dormancy was rare in this study. In four populations, plants were never observed to enter dormancy, and in no population was the incidence of dormancy greater than 5%. Further, the fate of dormant plants was similar to that of large 3-leaf plants (Knight 2004). For these reasons, dormant plants were grouped with large 3-leaf plants.

Fertility ($a_{16}$, the per-capita production of germinants by reproductive individuals) is the product of fecundity and germination probability, since both of these events occur within a one-year time step. The fates of reproductive and large 3-leaf plants are described by three underlying vital rates, the probability of growth ($g$), and the probabilities of reversion ($r_1$ and $r_2$).

$g$ = P[growth from stage 5 to stage 6]

$r_1$=P[reversion from stage 5 to stage 4 | no growth]

$r_2$=P[reversion from stage 6 to stage 5]

In our study, death was never observed for plants in the largest two stage classes; shrinking in size prior to death is typical for this species. We describe the population-level effects of deer herbivory in terms of its effect on these 3 underlying vital rates.

The matrix population model is $\mathbf{n}_{t+1}=\mathbf{A}*\mathbf{n}_t$, where the vector $\mathbf{n}_t$ gives the number of

individuals in each stage at time t. The asymptotic population growth rate, λ, is the dominant eigenvalue of **A**. λ determines whether a population can persist (λ≥1) or not (λ<1). The stable stage distribution (**w**) and the reproductive value (**v**) are the right and left eigenvectors of **A** corresponding to λ (Caswell 2001). The elasticity of λ to changes in the matrix element $a_{ij}$ is

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}} = \frac{\partial(\log\lambda)}{\partial(\log a_{ij})} \qquad 2$$

(de Kroon et al. 1986, Caswell 2001). Elasticities can be interpreted as how proportional changes in each element would affect λ.

For each population, we calculated λ separately for each year. We calculated 95% confidence intervals around λ using bootstrap resampling methods (McPeek and Kalisz 1993, Caswell 2001) as follows. The original demographic data set for each population and year includes information on the fate of every individual in the plots from one year to the next. A bootstrap data set was created by sampling individuals, with replacement, from the original demographic data set until the sample size of each bootstrap data set was identical to the original data set. A total of 1000 bootstrap data sets were generated for each population and year using MATLAB (2000) and the data from each bootstrap data set were used to calculate the elements of a **A**. All bootstrap matrices for a given population and year had identical values for $a_{16}$, (seed production * germination probability) and $a_{21}$ (germinant survival) because these values used data from seed baskets.

The effect of herbivory on the vital rates

We used linear regression to quantify the relationship between the three vital rates, $g$, $r_1$, and $r_2$, and the level of herbivory (percent of large 3-leaf plants consumed for $g$ and $r_1$, and percent of reproductive plants consumed for $r_2$). We performed separate regressions for each

year ($N$ = 12 populations), and an overall regression combining all data across the three years ($N$ = 12 populations * 3 years). The overall regressions assume that responses from the same population in different years are independent. Because the 95% confidence intervals for the slopes and intercepts of the overall and the yearly regressions overlapped, we present only the results from the overall regressions.

The fertility ($a_{16}$) is expressed per reproductive plant, but some of those plants will be consumed and not reproduce. Thus $a_{16}$ is also a function of herbivory;

$$a_{16} = 11.53 - 0.1153x$$

so that at 100% herbivory there is no reproduction and at 0% herbivory, fertility equals the value observed in the absence of herbivory across all populations and years.

Population-level effects of herbivory

To examine the change in λ, **w**, **v**, and $e_{ij}$ across a gradient of herbivory, we calculated these for the entire range of possible levels of herbivory (0-100%) at 1% intervals. At each level of herbivory, the matrix elements for the non-browsed stage classes are the mean for all populations and years, and the matrix elements for the browsed stage classes are based on the linear regressions on $g$, $r1$, $r2$, and $a_{16}$ and herbivory described above. We summed our elasticity results into 7 meaningful classes of elasticities: the fate of germinants ($e_{21}$), the fate of seedlings ($e_{32}$), the fates of 1-leaf plants ($e_{33}+e_{43}$), the fates of small 3-leaf plants ($e_{34}+e_{44}+e_{54}$), the fates of large 3-leaf plants ($e_{45}+e_{55}+e_{65}$), the fates of reproductive plants ($e_{56}+e_{66}$), and fertility ($e_{16}$).

Contributions of the vital rates

Because the level of herbivory is a quantitative variable, we used a LTRE regression analysis (Caswell 1996) to determine the contributions of each of the vital rates to the response

of λ to herbivory. Since herbivory affects λ only through its effects on *g*, *r1*, *r2*, and $a_{16}$, at any value of *x* we write

$$\frac{d\lambda}{dx} = \frac{\partial g(x)}{\partial x}\frac{\partial \lambda}{\partial g(x)} + \frac{\partial r1(x)}{\partial x}\frac{\partial \lambda}{\partial r1(x)} + \frac{\partial r2(x)}{\partial x}\frac{\partial \lambda}{\partial r2(x)} + \frac{\partial a_{16}(x)}{\partial x}\frac{\partial \lambda}{\partial a_{16}(x)} \qquad 3$$

The four terms of (3) give the contributions to the effect on λ of the responses of growth and reversion to herbivory. These contributions will be small if, at a given value of *x*, either herbivory has little effect on the vital rate or if λ is insensitive to changes in that vital rate. The derivatives $\partial g / \partial x$, $\partial r1 / \partial x$, and $\partial r2 / \partial x$ are obtained from the linear regressions shown in Figure 3. The sensitivities of λ to *g*, *r1*, and *r2* are obtained from the sensitivity of λ to the $a_{ij}$ using the chain rule. For this analysis, we scaled herbivory of the large 3-leaf plants (stage 5) with the herbivory of the reproductive plants (specifically, for every adult that is consumed, 0.71 large 3-leaf plants are consumed). Averaged over all populations and years, 0.71 stage 5 plants were consumed for each stage 6 plant.

The overall response of λ is obtained by integrating (3):

$$\lambda(x) = \int_0^x d\lambda + C \qquad 4$$

where the constant of integration C is set so that λ(*x*) passes through the mean observed herbivory level and the mean value of λ, to permit direct comparison with the linear regression in Figure 4, which also passes through this point. Integrating each term in (3) separately shows the response of λ contributed by each of the vital rates and by fertility.

## RESULTS

### Herbivory and the vital rates

Herbivory was highly variable among populations, ranging from 0% to over 60% of the

reproductive and large 3-leaf plants in the population (Table 1). In some populations, herbivory was consistently high (e.g. population TW) or consistently low (e.g. populations DC, DH, and DR), whereas other populations had variable levels of herbivory from year to year (e.g., population EL). Mortality due to herbivory was never observed for plants in either the large 3-leaf or reproductive stage (Appendix 1).

Herbivory affected the vital rates of large 3-leaf and reproductive plants. Overall, as the percent of plants consumed increased across populations, the probability of growth decreased and the probabilities of reversion increased (Fig. 2).

The average seed production of plants not consumed by deer across all populations and years was 14.5 (Table 1). The average germination probability per seed was 0.797 (Table 1). In *T. grandiflorum*, both of these events occur within one year, and therefore, the fertility ($a_{16}$) of plants not eaten by deer was 11.53 (the product of average fecundity and germination probability).

Population consequences of herbivory

The population growth rate ($\lambda$) declined as herbivory increased (Fig. 3). This relationship indicates that 14.5% is a threshold level of herbivory; when herbivory levels exceed 14.5%, the population is projected to decline towards extinction. The stable stage distribution (SSD) (**w**) varied with the level of herbivory across populations. As herbivory increased, the proportion of new recruits (plants in the germinant and seedling stage classes) decreased, and the proportion of individuals in two of the non-reproductive stage classes (small 3-leaf and large 3-leaf) increased (Fig. 4). The reproductive values (**v**) of plants in the largest 3 stage classes (small 3-leaf, large 3-leaf and reproductive) all decreased with increasing herbivory (Fig. 4). The reproductive values of plants in smaller stage classes were generally low, reflecting the low probability that these

individuals will survive to reproduction and the long length of time it takes for *T. grandiflorum* individuals to reach maturity. As herbivory increases, λ becomes more elastic to changes in the fates of small 3-leaf plants, and less elastic to changes in the fates of reproductive plants (Fig. 4). The elasticity of λ to fertility is never large, and declines to negligible values as herbivory increases (Fig. 4).

Contributions of the vital rates

The contributions of *g*, *r1*, *r2*, and $a_{16}$ to $d\lambda / dx$ are shown in Figure 5. They were most negative at small values of x; that is, herbivory had its greatest effects at low values, with diminishing marginal effects as the level of herbivory increased. All the contributions were of comparable magnitude, implying that none of the effects can be safely neglected in evaluating the population-level effect of herbivory.

## DISCUSSION

Populations of *T. grandiflorum* with high levels of herbivory had significantly higher probabilities that large 3-leaf plants and reproductive plants would regress in stage, significantly lower probabilities that large 3-leaf plants would advance to the reproductive stage, and lower annual fertility. These changes in vital rates caused a decrease in λ with increasing herbivory: the individual populations' λ ranged from stable or growing populations to those declining by 10% each year. Although our sites undoubtedly differed in unmeasured abiotic factors (such as light availability and proximity to roads), we find that the level of deer herbivory explains a significant portion of the variation in demographic vital rates and thus population growth rate across populations and years. Our study highlights how vitally important understanding and managing deer abundance is to the persistence of *Trillium grandiflorum*, and likely other

understory plants, that are similarly long-lived and palatable to deer.

A primary goal in the management of species of conservation concern is to understand and create conditions that can shift a population's growth rate from < 1.0 to > 1.0. Elasticities identify the parameters in which proportional changes will have the largest impacts on λ, and can therefore be used to pinpoint stages that are potential targets for conservation efforts (Crouse et al. 1987, Caswell 2000, 2001, Morris and Doak 2002, Bessinger and McCullough 2002). One concern in such applications is the robustness of the elasticities of λ to environmental changes, which determines whether the results from one population can be extrapolated to others. In most cases, the elasticities are remarkably robust (Caswell 2001). However, in this study we found that the elasticities of *T. grandiflorum* shift as a function of the incidence of deer herbivory; λ becomes more sensitive to changes in the fates of plant in the small 3-leaf stage as the level of herbivory increases. This is partly because, as herbivory increases, reproductive and large 3-leaf plants revert in stage, and the population becomes dominated by small 3-leaf plants at stable stage distribution. However, we note that over the range of herbivory for which the population can persist, the variation in elasticities among stages is much less.

Fertility had one of the lowest elasticities across the entire gradient of herbivory. Because of this low sensitivity, we find that changes in fertility contributed little to the change in λ across moderate levels of herbivory (0-30%) relative to changes in the fates of plants in larger stage classes (Fig. 9). The insensitivity of λ to changes in fertility in *T. grandiflorum* is consistent with other demographic studies on long-lived plants (reviewed by Silvertown et al. 1993), turtles (Heppell 1998), birds (Saether and Bakke 2000), and mammals (Heppell et al. 2000). In general, we expect that ecological interactions acting primarily on the fertility of long-lived organisms will have less of an influence on λ than those that affect other vital rates.

Our study provides a direct link between the intensity of deer herbivory and the persistence of *T. grandiflorum* populations. Under the environmental conditions where these data were collected, consumption of more than 15% of large 3-leaf and reproductive *T. grandiflorum* will cause the population to decline towards extinction. The critical level of deer herbivory that determines persistence or extinction will differ across *T. grandiflorum* populations, due to spatial variation in other environmental factors that affect the demography of this species (e.g., soil quality, light; Schmucki1 and de Blois 2009). However, the critical level of 15% is well supported by our analyses, and this value can provide a reasonable guide for managers monitoring the health of the forest understory. Eight of our 12 *T. grandiflorum* populations experienced herbivory greater than 15% in at least one of the 3 years of study, indicating that current levels of herbivory are high enough to pose significant extinction risks to many of these populations (see also Knight 2004). Other studies on *T. grandiflorum* have reported similar high levels of herbivory. In northern Wisconsin, Rooney and Gross (2003) found that between 4-24% of the reproductive and non-reproductive *T. grandiflorum* were eaten by deer, while in southeastern Minnesota, Augustine and Frelich (1998) found that 24-77% of the reproductive plants were grazed. If our results from northwestern Pennsylvania are indicative of the effects of herbivory on *T. grandiflorum* in general this once-common understory species could be in danger of regional or even global extinction. This species is likely a bellwether of future declines of other long-lived herbaceous perennial members of the understory community.

Ours is the first study to apply a regression LTRE analysis to a natural population. The relationship between herbivory and $\lambda$ revealed by this analysis is non-linear. This non-linearity buffers the population from rapid decline at high levels of herbivory, because the population becomes dominated by small, non-flowering stages that deer do not consume. This result may

explain the dissonant facts that *T. grandiflorum* are a preferred food for deer, but remain present and even abundant in many areas. The long-lived nature of *T. grandiflorum*, the slow rate of decline due to this non-linear buffer, and the large number of individuals in some populations means that local extinctions will take a long time to occur, but that these extinctions are inevitable. Our analyses demonstrate that even common, abundant and demographically robust plants such as *T. grandiflorum* cannot sustain high levels of deer herbivory in the long run.

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**Table 1.** Vital rates and % herbivory for 12 populations of *Trillium grandiflorum*. Fecundity is the annual average number of seeds per reproductive individual in a population (sample size). Only plants not consumed by deer are reported. Seed germination and seedling emergence probabilities were calculated from seed baskets planted in 1999 in each population. Germination probability is the proportion of seeds that survive and germinate in the soil after one year, and seedling emergence probabilities are the proportion of seeds that survive two years in the soil and produce a cotyledon in the second spring. The percent of reproductive and large 3-leaf individuals consumed by deer in each population and year are presented in the last six columns.

| **Population** | **Fecundity** | | | **Germination probability (yr 1)** | **Seedling emergence (yr2)** | **% Herbivory – Reproductive Stage** | | | **% Herbivory – Large 3-Leaf Stage** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1999 | 2000 | 2001 | | | 1999 | 2000 | 2001 | 1999 | 2000 | 2001 |
| **DC** | 18.8 (6) | 13.7 (34) | 16.8 (27) | 0.80 | 0.16 | 1.3 | 0 | 0 | 0 | 0 | 0 |
| **DH** | 7.7 (7) | 12.3 (46) | 20.6 (22) | 0.83 | 0.17 | 11.5 | 0 | 4.88 | 0 | 2.74 | 4 |
| **DR** | 25.1 (7) | 16.3 (10) | 24.4 (23) | 0.57 | 0.20 | 0 | 0 | 0 | 0 | 0 | 0 |
| **EL** | 9.6 (8) | 10.6 (16) | 11.2 (38) | 0.78 | 0.18 | 0 | 51.35 | 25.0 | 0 | 53.75 | 2.74 |
| **FX** | 10.3 (7) | 9.9 (16) | 10.5 (23) | 0.90 | 0.06 | 51.2 | 37.84 | 16.67 | 8 | 22.64 | 12.77 |
| **GT** | 9.3 (13) | 10.6 (15) | 12.6 (10) | 0.86 | 0.20 | 36 | 5.56 | 18.75 | 0 | 6.8 | 37.68 |
| **LR** | 9.6 (5) | 12.1 (34) | 15.3 (19) | 0.83 | 0.26 | 0 | 0 | 10.7 | 0 | 19.23 | 6.25 |
| **RH** | 12.8 (9) | 15.3 (43) | 17.4 (27) | 0.77 | 0.21 | 28.36 | 14.8 | 8.95 | 5.58 | 12.28 | 5.56 |
| **RM** | 10.6 (8) | 12.7 (15) | 14.3 (20) | 0.75 | 0.23 | 7.7 | 20.8 | 5.88 | 10 | 50 | 30.77 |
| **TW** | 10.6 (44) | 8.3 (27) | 11.4 (19) | 0.79 | 0.40 | 56.3 | 59.1 | 26.45 | 32.85 | 13.1 | 16.05 |
| **WC** | 22.6 (11) | 20.2 (44) | 25.0 (31) | 0.89 | 0.40 | 2.0 | 24 | 6.25 | 0 | 9.6 | 15.2 |
| **WH** | 15.4 (10) | 18.1 (25) | 18.7 (18) | 0.79 | 0.31 | 41.67 | 60.7 | 8.7 | 15.07 | 63.85 | 0 |

FIGURE LEGENDS

**Figure 1**. Life cycle graph of *Trillium grandiflorum*. Stages are germinant (1), seedling (2), 1-leaf plant (3), small 3-leaf plant (4), large 3-leaf plant (5), and reproductive plant (6). Arrows represent transitions from one stage class to the next in a one-year time step. Mean transitions across all populations and years are shown for the stage classes that are not browed by deer. For the largest two stage classes, transitions depend on deer herbivory.

**Figure 2**. The relationship between the vital rates of large 3-leaf and reproductive *T. grandiflorum* and the percent herbivory on plants in those stage classes. The vital rates are: $g$, the growth rate of large 3-leaf plants, $r_1$ and $r_2$, the reversion rates of large 3-leaf and reproductive plants (respectively).

**Figure 3**. The relationship between population growth rate ($\lambda$) and herbivory in *T. grandiflorum*. Data are shown for 12 populations and 3 years. The average % herbivory is the mean of the % herbivory on reproductive and on large 3-leaf stages. The line integrates the contributions from the regression LTRE analysis.

**Figure 4**. The relationship between the stable stage distribution (SSD; top figure), reproductive value (middle figure), and summed elasticities (bottom figure) of *T. grandiflorum* and percent herbivory. Summed elasticities include: (1) fate of germinants, seedlings and 1-leaf plants ($e_{2,1}$, $e_{3,2}$, $e_{3,3}$, $e_{4,3}$), (2) fate of small 3-leaf plants ($e_{3,4}$, $e_{4,4}$, $e_{5,4}$), fate of large 3-leaf plants ($e_{4,5}$, $e_{5,5}$, $e_{6,5}$), fate of reproductive plants ($e_{5,6}$, $e_{6,6}$), and fertility ($e_{1,6}$).

**Figure 5**. LTRE contribution of each of the vital rates $g$, $r_1$, $r_2$, and $a_{16}$ to the effect of herbivory on population growth rate.

Figure 1.

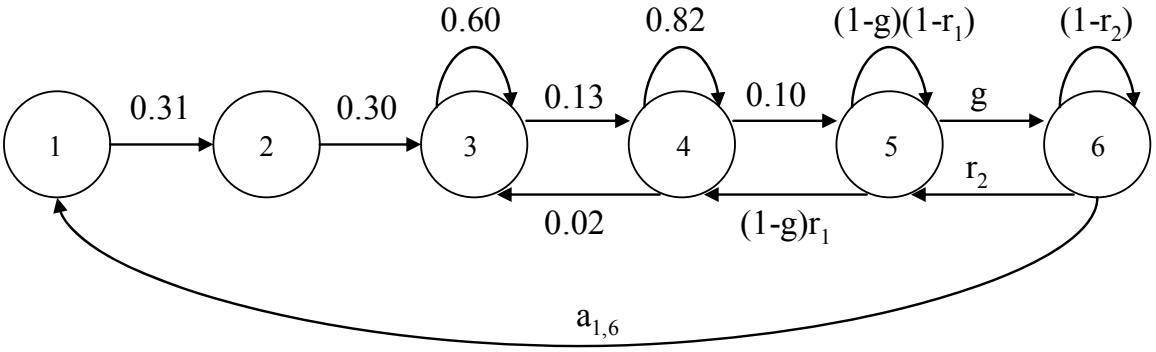


Figure 2.

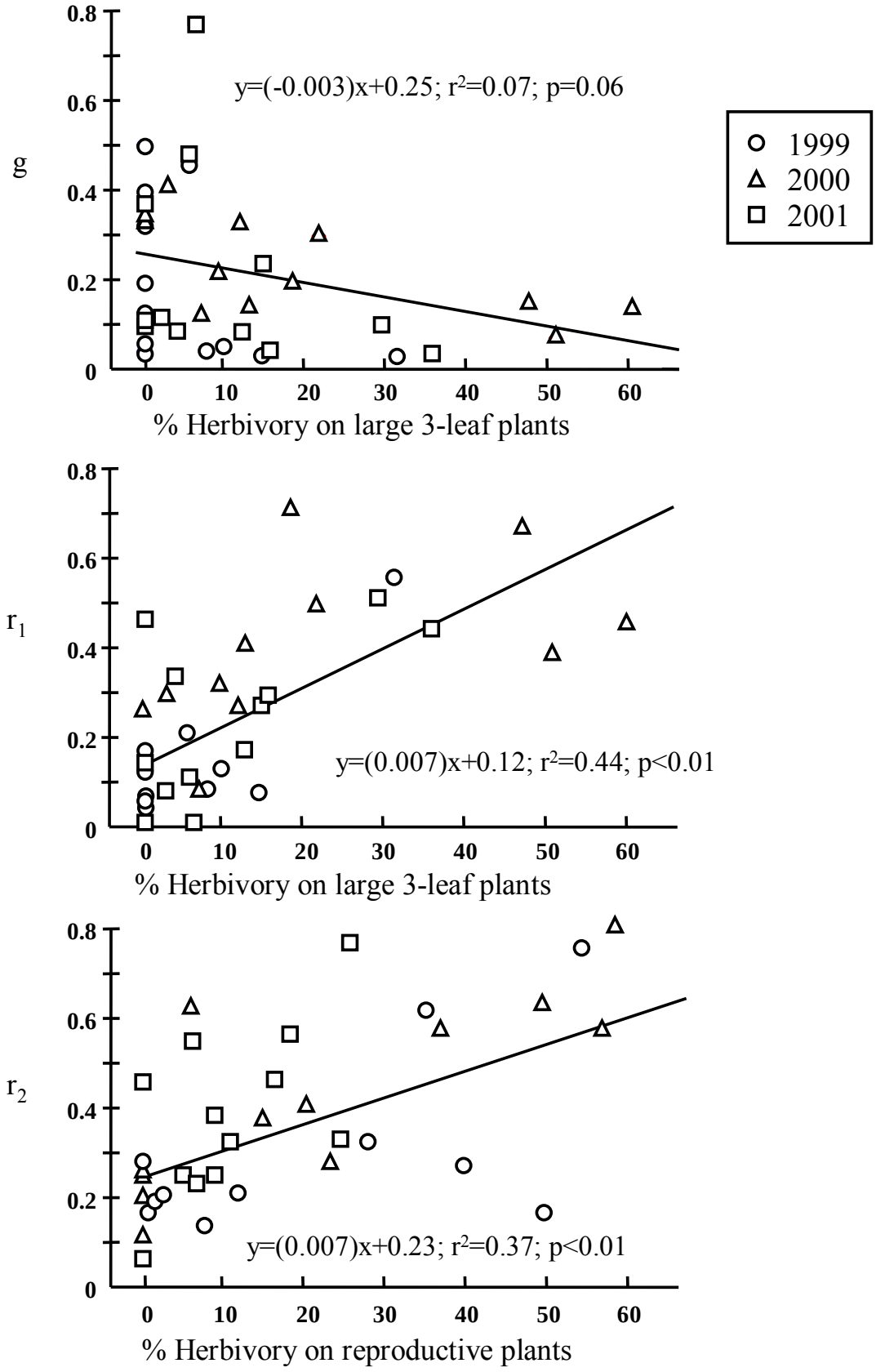

y=(-0.003)x+0.25; r²=0.07; p=0.06
g
1999
2000
2001
% Herbivory on large 3-leaf plants
y=(0.007)x+0.12; r²=0.44; p<0.01
r1
% Herbivory on large 3-leaf plants
y=(0.007)x+0.23; r²=0.37; p<0.01
r2
% Herbivory on reproductive plants

Figure 3.

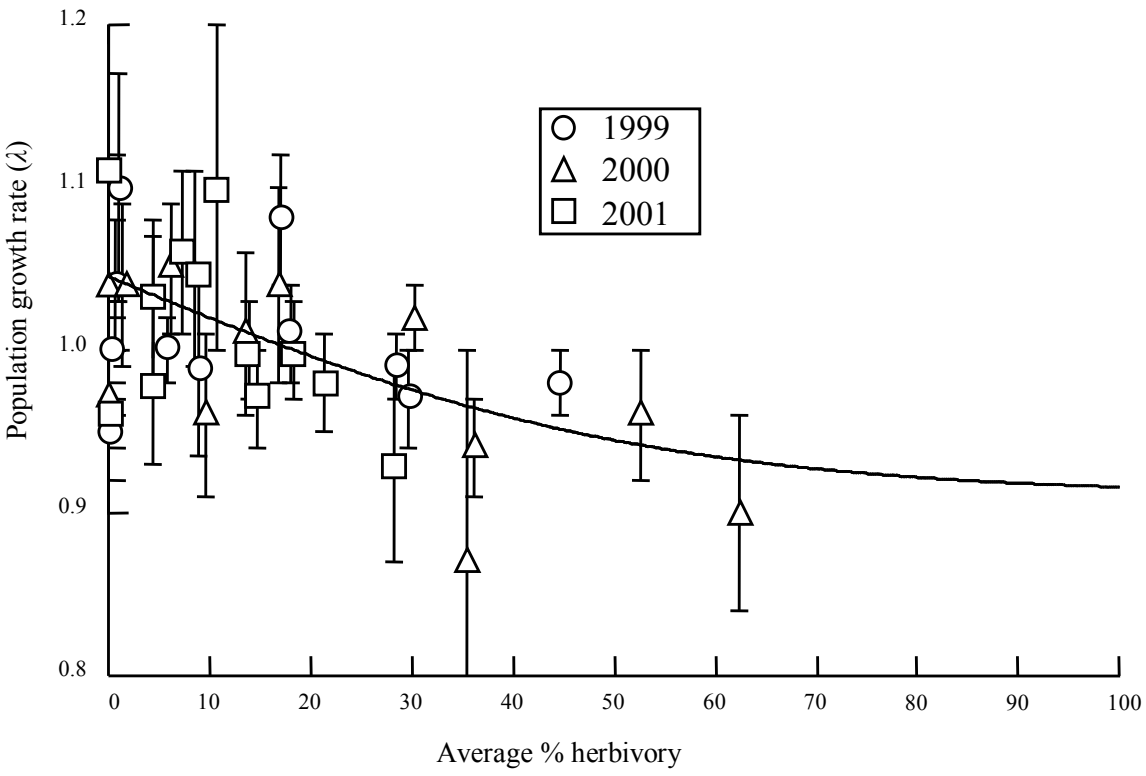

1.2
1.1
1.0
0.9
0.8
Population growth rate (λ)
1999
2000
2001
0
10
20
30
40
50
60
70
80
90
100
Average % herbivory

Figure 4.

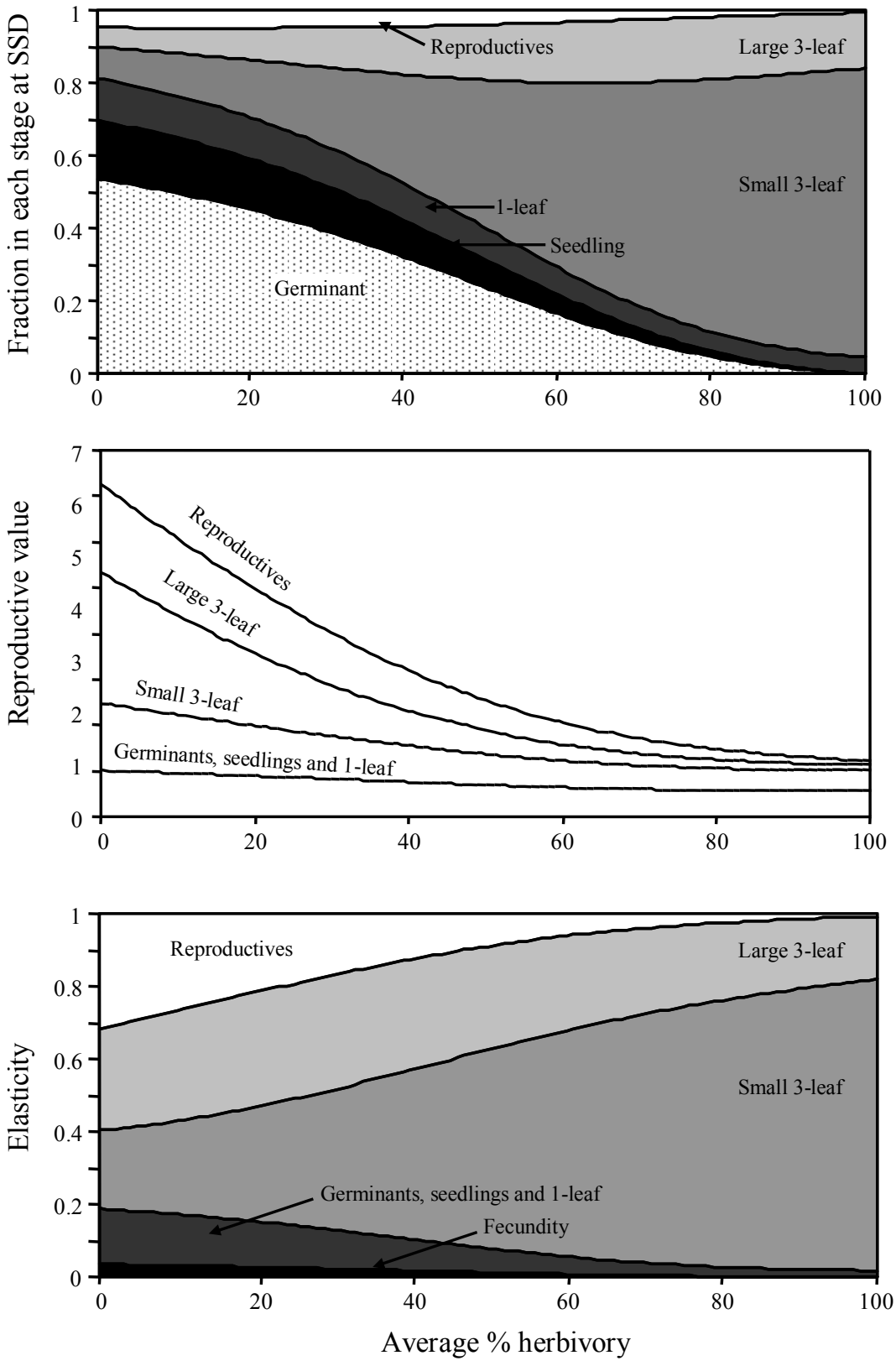
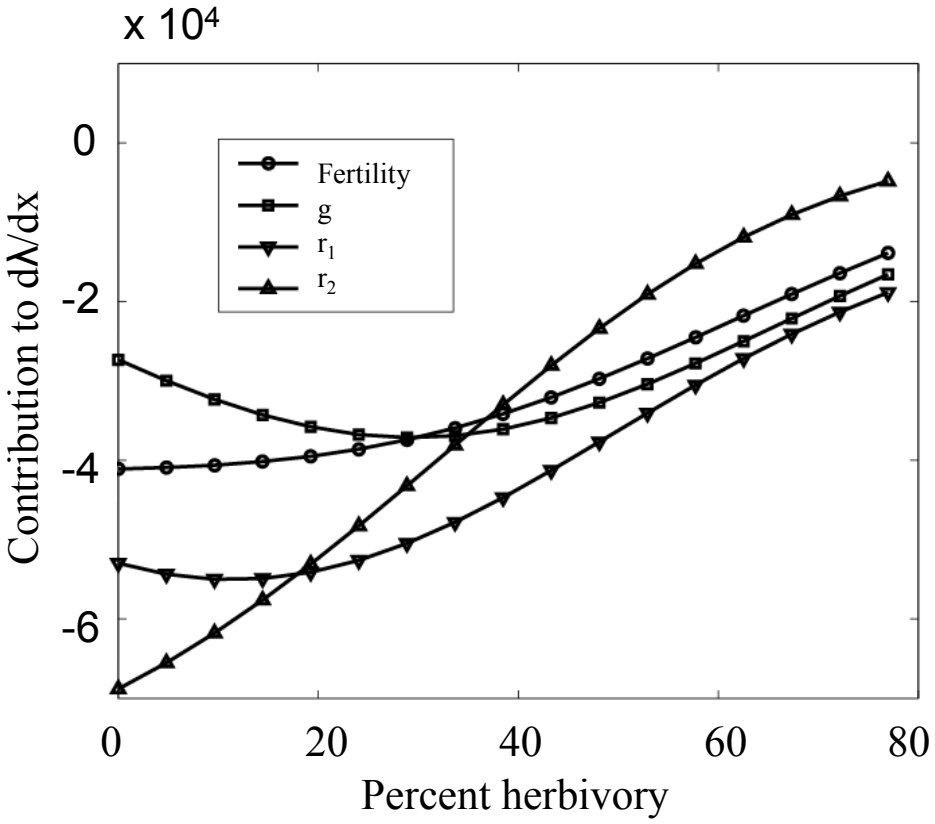

Fraction in each stage at SSD
Reproductives
Large 3-leaf
Small 3-leaf
1-leaf
Seedling
Germinant
Reproductive value
Reproductives
Large 3-leaf
Small 3-leaf
Germinants, seedlings and 1-leaf
Elasticity
Reproductives
Large 3-leaf
Small 3-leaf
Germinants, seedlings and 1-leaf
Fecundity
Average % herbivory

Figure 5.


x 10⁴
0
-2
-4
-6
Contribution to dλ/dx
Fertility
g
r1
r2
0
20
40
60
80
Percent herbivory